Summer behavior of Atlantic walruses *Odobenus rosmarus rosmarus* (L.) at Coats Island, N. W. T. (Canada)

By E. H. Miller and D. J. Boness

Vertebrate Zoology Division, B. C. Provincial Museum, and Biology Department, University of Victoria, and National Zoological Park, Smithsonian Institution, Washington

Receipt of Ms. 9. 11. 1982

Abstract

This paper describes counts, group size, structure, and composition, behavior (especially nursing), and airborne acoustic signals of summering Atlantic walruses in northern Hudson Bay. The significance of the findings to understanding of socioecology of pinnipeds is discussed, and the need for coordinated, synchronized research at several hauling grounds in the vicinity is emphasized.

Introduction

Knowledge of social behavior in pinnipeds, and appreciation of its evolutionary and ecological significance, have increased greatly in recent years. Important gaps in understanding remain, notably for species which associate with ice during all or part of the annual cycle, and which are highly aquatic (viz. Odobenidae and many species of Phocidae; Stirling 1983).

Walruses, *Odobenus rosmarus* (L.), are particularly important for understanding the evolution and ecology of pinniped social systems, because the single extant species is a phyletic relict, widespread, and the only member of the otariid-odobenid stock which associates appreciably with ice (Burns 1970). Our meager knowledge of walrus behavior reflects this association, since the range and seasonal movements of walruses are closely tied to ice movements (Fay 1981, 1982), making field studies very difficult. Further, walruses mate in late winter, when they are accessible to man only by ice-breaking vessels. Improved knowledge of walrus society is particularly important now, because the species reproduces slowly (Fay 1982; Mansfield 1958), and is being increasingly affected by development in the arctic (Davis et al. 1980). Such a consideration applies especially to the small walrus populations in Kara Sea/Novaya Zemlya, Svalbard/Franz Josef Land, eastern Greenland, and the Canadian arctic (Fay 1982). In the latter region, walruses are scattered and many may exist in small, relatively isolated sub-populations (see Davis et al. 1980 and Reeves 1978). Demographic and reproductive characteristics of the Canadian walrus population may differ significantly from the relatively well known population of the Bering and Chukchi Seas, considering the differences in appearance, body size, levels of exploitation, food base, population size, and population subdivision. Documentation of population and reproductive biology of Canadian walruses is therefore very important.

We spent parts of two summers on Coats Island (62° 23′ N 82° 11′ W), northern Hudson Bay, Canada, to study walruses. Several traditional haulout sites exist in the vicinity, and are used by walruses in late summer and early fall, in the absence of sea ice. Unlike the well known hauling ground of males at Round Island, Alaska (Miller 1975a, 1975b, 1976), those at Coats Island are used by both sexes and various ages. The purposes of our study

U.S. Copyright Clearance Center Code Statement: 0044-3468/83/4805-0298 $ 02.50/0
Z. Säugetierkunde 48 (1983) 298–313

ISSN 0044-3468 / InterCode: ZSAEA 7

were to estimate herd size and composition (with particular reference to dependent young), to describe social behavior (particularly of females and their offspring), and to record in-air vocalizations.

Methods and materials

We established camps near different hauling grounds in the two years of study (1978, 1980). In 1978, camp was established on the SE coast, about 600 m from a hauling ground where most previous studies have been made (Loughrey 1959; Mansfield 1958; Miller 1982). The site is a low rock promontory adjacent to a boulder beach, both of which are used by walruses during haulout, though

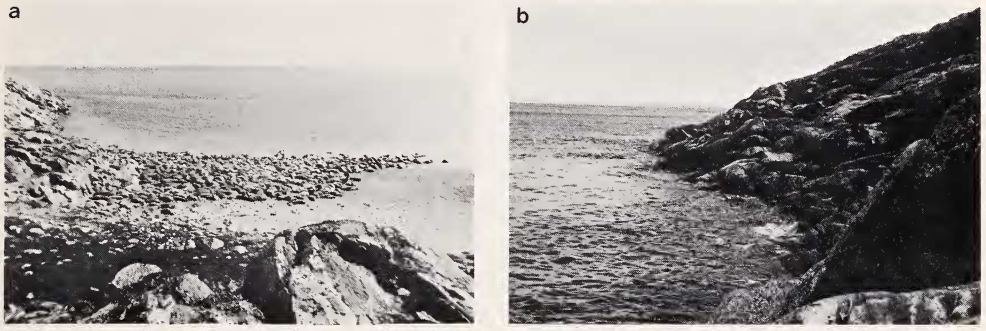

Fig. 1. a: View of the sand beach at the northern hauling ground, from an inland observation point. The southern edge of the promontory is visible (31 July 1980); b: View of the northern side of the northern hauling ground, from an inland observation point. A small group of walruses is visible (29 August 1980)

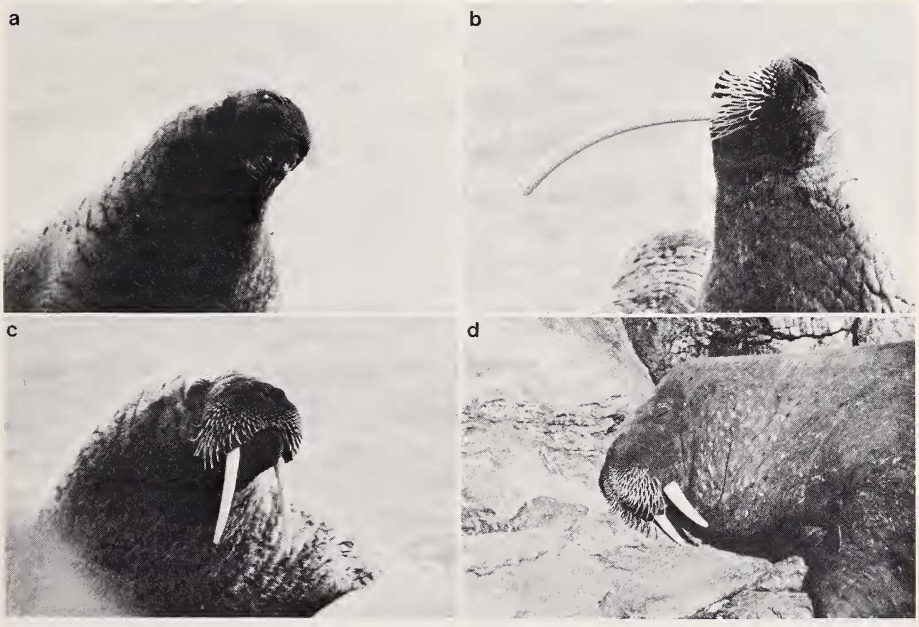

Fig. 2. a: One-year-old dependent young (C2); b: Large adult female; c: Medium-sized adult female; d: Small male. Note the depth of the tusks at the base and the small healed scratches (pale areas) on the neck of the male, as compared with the female in c

the promontory is favored (especially by females and their young; Fig. 1 of Miller 1982). The 1980 study location was farther north, near Cape Pembroke. It was also a rock promontory, though steeper and higher than the other site, and was adjacent to a sand beach (Fig. 1). Walruses hauled out most frequently on the promontory, though the largest herds formed on the beach. The 1978 study was from 23 July to 8 August; that in 1980 extended from 28 July to 2 September. Observation distances from walruses on land averaged 50–100 m, but were greater from walruses at sea. Some close-up observations were made by approaching the walruses from downwind, and audio recordings were thus made over short distances (5–20 m).

Audio recordings were made at 19 cm per sec on Scotch tape 208, matched to a Nagra IS tape recorder and Sennheiser MKH 816 "shotgun" microphone with wind sock. Sound spectrograms were prepared on a Kay Elemetrics Sona-Graph 7029A.

Walrus groups in the water were classified into three broad activity categories: Reconnoitering – group swimming slowly toward land or along a beach, as though prospecting for a haulout site; Travelling – group swimming actively and directedly; and Rafting – group not actively moving, and with most group members sleeping, nursing, etc. (Fig. 4).

Several external features of males change with age: overall body size; tusk length; depth of the tusks near the base; massiveness of the face, head, and neck; and characteristics of the skin and hair (old, large animals tend to have heavily scarred, nearly naked, lightly or patchily pigmented, rugose necks, while small, young animals have well haired, lightly scarred, darkly pigmented, smooth necks; see Fay 1981, 1982). It is harder to judge the age and size of females, because they vary less in size than males, have more slender tusks, and are darkly colored and well haired throughout life. In this study, we did not distinguish among age (size) classes of adults (defined as animals other than dependent young). Dependent young included those born that year (calves – C1), one-year-olds (C2), and two-year-olds (C3): C1 – small, very dark in color, no tusks visible; C2 – larger, coat lighter and browner than C1, no tusks visible except when the mouth is opened or seen from a favorable aspect; C3 – larger, similar coat color to C2, tips of tusks visible even when the mouth is closed (see Fay 1982; Loughrey 1959; Mansfield 1958). Examples of these classes are shown in Figs. 2 and 4.

Results

Counts

Walruses were on land in low numbers (300, declining to 0) on 23 and 24 July 1978, then were absent until 5 August because sea ice suitable for haulout was present until then, and were present in high numbers (increasing to 1500+) on 5–8 August.

In 1980, no walruses were seen (from boat) on or near the southern hauling ground on 28 July, but 338 were on the promontory at the Cape Pembroke haulout site on that date. Numbers declined to about 80 on the following day, and on 30 July rose to about 130. Walruses also started hauling out on the beach on 30 July, reaching about 100 in number. By 0500 h on 31 July, no walruses remained on the north side of the promontory but numbers on the beach reached about 500. That night, a polar bear killed a calf and all walruses left land. The next date on which walruses hauled out was the night of 28–29 August, when 32 animals hauled out on the promontory. They left on 29 August, due to disturbance from an airplane and a dog. No other walruses hauled out on land before we left, on 2 September.

As with haulout patterns on land, on some days in 1980 many walruses were present in the water, and on other days there were few. At extremes, we sometimes saw no walruses all day even with excellent visibility (clear skies, calm sea), while at others we saw hundreds close to shore under much worse weather conditions.

Herd composition and spatial organization: Land

Detailed estimates of herd composition on land were only possible in 1978. Detailed data are presented elsewhere (Miller 1982), and we only summarize them here.

Along the seaward margin of the beach and promontory, 624 adult and juvenile walruses were classified. These included 17 males (3 % of adults) and 594 females (97 %). About 85 % of the females were with dependent young, and roughly 46 % of the dependents were calves. In contrast, in central locations and on top of the promontory, 206

males (18 % of adults) and 947 females (82 %) were counted, 82 % of the females were with dependent young, and only 34 % of the dependents were calves. Overall, there was a clear tendency for females to predominate on the promontory more than elsewhere, and in the seaward margins of the herd more than in central and inland parts. These trends were strongest for females attending calves.

Group composition: Sea

In 1980, we estimated composition of 571 groups in the water, which included 2030 walruses. Most estimates were incomplete, since some walruses were usually below the water's surface, and the movements of others made classification difficult. Dependent young and large males were the easiest to identify, and most of the following remarks pertain to them. Identification of females was biassed because they were often only distinguished by their association with dependents.

Group size ranged from 1 to 26 ($\overline{Y} = 3.56$, median = 2.37), and about 54 % of all groups contained 1–2 walruses (Fig. 3). Group size varied with major activity class: 150

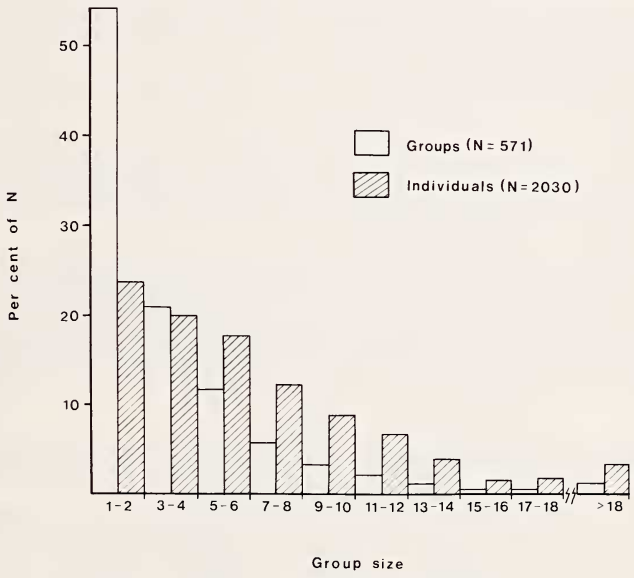

Fig. 3. Frequency histograms of group size in the water showing the per cent of groups and the per cent of individual walruses corresponding to different group sizes

Rafting groups averaged 4.47 walruses (median = 3.03), while 183 Travelling herds averaged only 2.63 (median = 2.15). Reconnoitering groups were intermediate ($\overline{Y} = 2.81$, median = 2.18, N = 48).

Size of groups also varied according to their composition. The average size of 206 groups with dependent young was 4.68 (median = 3.64), as compared with 2.86 (median = 2.62) for 49 groups with males. This difference partly reflects the tendency for males to occur outside Rafting groups, and for dependent young to occur in them: only about 17 % of males were seen in the larger Rafting groups, while about 53 % of dependent young were identified there (Table 1). Despite this bias, males were noted in smaller groups than were dependents within activity classes, as well: the mean size of 67 Travelling groups with dependents was 3.55 (median = 2.69), while that for 20 groups with males was 2.45 (median = 2.50); and the mean size of 61 Rafting groups with dependents was 5.85

Table 1

The incidence of dependent young and males in groups at sea, as related to major group activity[1]

	Activity Class			
	Travel	Raft	Reconnoitre	Unknown
C1	*17*, 55 (*18*, 55)	*8*, 26 (*9*, 27)	*6*, 19 (*6*, 18)	*0*, – (*0*, –)
C2	*15*, 28 (*16*, 29)	*26*, 49 (*28*, 50)	*12*, 23 (*12*, 21)	*0*, – (*0*, –)
C3	*10*, 30 (*12*, 32)	*15*, 45 (*16*, 43)	*8*, 24 (*9*, 24)	*0*, – (*0*, –)
Total Dep. young[a]	*65*, 44 (*85*, 36)	*63*, 43 (*125*, 53)	*20*, 14 (*28*, 12)	*58*, – (*105*, –)
Males	*20*, 43 (*30*, 39)	*10*, 21 (*13*, 17)	*17*, 36 (*34*, 44)	*2*, – (*4*, –)

[1] Entries are *number* and per cent of occurrences, followed by (in parentheses) *number* and per cent of walruses. Per cent figures are excluded from the "Unknown" column. – [a] Including dependents of undetermined age.

(median = 5.40), compared with 3.08 for 12 groups with males (median = 2.50). All identified males, but only 69 % of identified dependents, were in Travelling groups of five or fewer walruses. Similarly, all males were seen in Rafting groups of six or fewer, but only 47 % of dependents were identified there.

This suggestion of segregation between dependent young and males can be viewed differently. Consider the number of joint and separate occurrences of groups with dependents or males, or both (Table 2). There were 248 groups in which dependents or males (or both) were identified. Dependents were seen in 206 of these groups and males in 49, but dependents and males were identified in the same group only seven times.

Table 2

Joint and separate occurrences of dependent young (DY) and males in groups at sea, as related to major group activity

Activity class	Number (and percentage) of groups with DY only	Males only	DY or males only	DY and males	Totals
Travel	63 (75.9)	18 (21.7)	81 (97.6)	2 (2.4)	83
Raft	60 (85.7)	7 (10.0)	67 (95.7)	3 (4.3)	70
Reconnoitre	18 (51.4)	15 (42.9)	33 (94.3)	2 (5.7)	35
Totals[a]	199 (80.2)	42 (16.9)	241 (97.2)	7 (2.8)	248

[a] Including groups whose major activity was not noted.

Individual behavior

General activities of walruses on land have been described elsewhere, and little needs to be added here (Miller 1975a, 1975b, 1976; Salter 1978, 1979, 1980). Diverse individual behavior occurs in the water. Walruses Travelling in the water generally alternate Deep Dives with periods at or just below the surface (Surface Travelling). The latter consist of one (usually) to several breaths immediately after surfacing from a Deep Dive, followed by shallow submersion or submersion of just the face. Several alternations of breaths and submersions may occur, or walruses may just breathe once then Deep Dive again. Deep Dives show no age- or sex-associated trends in duration. They averaged 0.66 min long (S.E. = 0.048, g_1 (skewness) = 2.2, N = 289). Surface Travelling likewise shows no trends according to age or sex, and averaged 0.21 min long (S.E. = 0.019, $g_1 = 3.7$, N = 249). Thus Travelling groups spent about 76 % of their time below the surface in Deep Dives.

Walruses in Reconnoitering groups engaged in variable, ill defined dives and other activities at the water's surface, and often milled about just offshore. We gathered no quantitative data on act durations for such groups.

Individual behavior was most diverse in Rafting groups. Walruses swam slowly, irregularly, and in undirected fashion, at and below the surface, and such Surface Swimming often merged into Shallow Dives. These categories include highly variable behavior, and are probably aggregates of clearer act types which could not be distinguished because of observation conditions. Descriptive statistics follow: Surface Swim – $\overline{Y} = 0.22$ min, S.E. = 0.028, $g_1 = 10.2$, N = 233; Shallow Dive – $\overline{Y} = 0.37$ min, S.E. = 0.033, $g_1 = 2.5$, N = 192.

Walruses at rest in Rafting groups assumed one of several postures. Most commonly,

Table 3

Lone activities of walruses in Rafting groups: descriptive statistics

Activity	Walrus class[a]	$\overline{Y} \pm$ S.E. (g_1)[b]	N
Ventral and Side Float[c]	Adult	0.61 ± 0.066 (3.4)	275
	DY[d]	0.31 ± 0.030 (2.5)	140
Bottle[e]	Adult	0.85 ± 0.168 (3.0)	65
	DY[f]	0.55 ± 0.117 (2.2)	32
Up	Adult	0.28 ± 0.032 (2.3)	97
	DY[g]	0.30 ± 0.044 (2.6)	98
Head Lift	Adult	0.14 ± 0.044 (16.6)	320
	DY[g]	0.12 ± 0.014 (3.5)	112

[a] DY = Dependent young. – [b] $\overline{Y}$ = mean, S.E. = standard error (both in minutes), and g_1 = coefficient of skewness. All estimates of skewness deviate significantly from 0 ($p \leq 0.05$). – [c] For Back Float, $\overline{Y} = 0.29$ min (S.E. = 0.231, N = 22 adults). – [d] For C1, C2, and C3, $\overline{Y} = 0.19, 0.36$, and 0.41 minutes, respectively (S.E. = 0.025, 0.065, and 0.086, and N = 45, 48, and 23). – [e] Excluding Bottling by nursing females. – [f] For C1, C2, and C3, $\overline{Y} = 0.25, 0.32$, and 0.90 minutes, respectively (S.E. = not computed, 0.054, and 0.278, and N = 2, 18, and 10). – [g] No age-associated trends in durations occurred.

Fig. 4. Portion of a Rafting group, with Nursing females visible in the foreground and left background. Both of their offspring are Nursing while upside-down; the rump, tail, and ankles of the dependent in the foreground are visible. Note also the small male (behind female in foreground), with his very short but deep tusks, the one-tusked female in Up posture (right foreground), and the female Head-Lifting (right background)

they lay roughly horizontally, with face and hind quarters submerged, and only part of the central back exposed (Ventral Float). Walruses sometimes floated in a similar manner but on their side (Side Float), and rarely they floated on their back (Back Float, in adults only). Back Floats averaged 0.29 min long, and Ventral Floats averaged 0.61 min long for adults, and 0.31 min for dependent young (Table 3). Side Floats occurred infrequently, and we obtained no estimates of their duration. Ventral Floats were considered to be terminated each time a walrus Head-Lifted to breathe (Fig. 4). Head-Lifts usually lasted for only one breath, but they occasionally occurred in multiples with brief Ventral Floats between. They averaged 0.14 min long in adults and 0.12 min in dependent young (Table 3).

A very different resting posture, Bottle, was also common among adults in Rafting groups. Walruses remained motionless with the body upright, and only the head and upper neck exposed; the head was usually thrown back so that the tusks were parallel to the water surface. This was the usual posture of nursing females (Fig. 4). Dependent young seemed to have trouble remaining in a Bottling posture, and often made adjustments; this is reflected in the absence of observations of Bottling calves, and the briefer durations for dependents than adults (0.55 min vs. 0.85 min; Table 3). Bottling often merged into an oblique posture, Up, in which the body angle was about 45° relative to the water surface and the face was out of the water (and not usually strongly directed up) (Fig. 4). Dependent young and adults did not differ significantly in duration of Up (0.30 min for dependents, 0.28 min for adults; Table 3). Though Up was intermediate between the Bottle and the Ventral Float, it actually seemed to be a fairly discrete category, and it was usually easy to place walruses in one of the three main classes of rest postures.

Grooming (including scratching and rubbing) occurred much less often in the water than on land, and was recorded only once in our quantitative samples. On land, much Grooming is in the form of scratching with the rear flippers, dog-fashion, and also rubbing various body parts with the foreflippers. Most aquatic grooming is only rubbing the body with foreflippers. Likewise, Lone Play by dependent young was rare, and we saw none in sampling periods. It generally consisted of brief series of spasmodic, whole-body movements at the water's surface, or quick shallow dives, and often immediately followed Social Play.

Social behavior (except nursing)

Few overt social interactions occurred in Travelling groups, though naso-nasal Greetings were sometimes seen just below or at the water's surface (see descriptions in Miller 1975a). Also, dependents (especially calves) would occasionally Ride on the mother's back in slowly Travelling groups (especially at the water's surface); Mansfield (in litt.) has described similar behavior shown by immature males toward adult males. The same sort of interactions prevailed in Reconnoitering groups. When two Reconnoitering or Travelling groups met, or when a Travelling group joined Rafting animals, there was a flurry of naso-nasal Greetings, tactual contacts, and occasional tusk-threats.

Altogether, social activities comprised only about 1.1 % of the time of walruses in Travelling groups (2 % of act-type occurrences), and 0.1 % of the time of walruses in Reconnoitering groups (1 % of act-type occurrences) (Table 4). This difference is biassed, because males were watched more often in Reconnoitering than in Travelling groups, and they generally interacted less than females and dependents did. We felt that animals in Reconnoitering groups engaged in social activity with one another quite often, as they milled or travelled slowly. In 1978, males spent much time interacting with one another (and with females?) in the water just off the north side of the promontory. This included mock courtship and mounting, rubbing against one another, and sounds unique to such aquatic interactions (see Fay 1982; Miller 1975b; Ray and Watkins 1975). Such behavior was not seen or heard in 1980, presumably because it normally takes place in water adjacent to herds on land or ice. Rafting groups provide the greatest opportunity for repeated and prolonged interactions among walruses in the water, especially dependent young, and between offspring and their mothers. Dependents would often Ride on the mother's back while she swam slowly, or Climb on her in an undirected manner, Hold onto her passively with the foreflippers (usually while she Bottled), or would lean against her, rub against her, or place a foreflipper against her in Active or Passive Contact. They also often Nuzzled the mother by rubbing the face against her, or by tactually and/or olfactorily investigating her (excluding naso-nasal Greetings, in a strict sense). Most of these behaviors sometimes occurred between unrelated animals, as well. Finally, dependents Nursed in the water. The two other main kinds of social activity in the water were: Agonistic Behavior (aggression, usually in the form of tusk-threats, etc.; and submission, usually with bellowing, whisker erection, etc.; see Miller 1975a, 1975b); and Social Play between dependent young (jousting, diving and wrestling together, chasing, etc.).

Dependents in Rafting groups spent about 54 % of their time in social activities, mostly with their mothers. Excluding mother-offspring interactions, dependents spent about 8 % of their time in social behavior (mostly Social Play; Table 4). Females spent about 36 % of their total time in social activity, but only about 1 % in social activity unrelated to their own offspring (Table 4). Overall, social activities comparised about 38 % of the time of

Table 4

Percent time and occurrences spent in social activities[1]

	Major Activity Class			
	Travel	Reconnoitre	Raft	Means[a]
Males	*0*, 0 (*19.2*, 27)	*0.5*, 2.3 (*15.0*, 44)	*0.1*, 0.5 (*113.6*, 203)	*0.1*, 0.7 (*147,8*, 274)
Females	*1.1*, 2.5 (*89.3*, 203)	*0*, 0[b] (*16.0*, 77)	*1.2*, 2.3[c] (*415.4*, 782)	*1.1*, 2.2 (*520.7*, 1062)
Adults	*0.9*, 2.0 (*110.5*, 245)	*0*, 0[b] (*31.0*, 121)	*0.9*, 2.8[c] (*548.4*, 1024)	*0.9*, 2.4 (*689.9*, 1380)
Dep. young	*0.1*, 2.1 (*78.9*, 187)	*0.1*, 1.8[b] (*25.8*, 113)	*7.7*, 6.7[c] (*408.6*, 878)	*6.1*, 5.5 (*513.3*, 1178)
Totals	*1.1*, 2.1 (*189.5*, 432)	*0.1*, 0.9[b] (*56.8*, 234)	*3.8*, 4.0[c] (*957.0*, 1902)	*3.2*, 3.4 (*1203.3*, 2568)

[1] Sample sizes in brackets are in *walrus-minutes of observation* (first entry) and number of observed occurrences (second entry). – [a] Means weighted by sample sizes. – [b] Excluding interactions (including nursing) between females and their offspring. With those data included, figures are: 11.4, 9.1 (females); 6.2, 6.6 (adults); 2.5, 8.1 (dependents); and 4.6, 7.3 (totals). – [c] As for preceding footnote: 35.5, 16.9 (females); 26.8, 13.1 (adults); 54.0, 27.9 (dependents); and 38.4, 19.9 (totals).

Table 5

Affiliative and contact behavior of dependent young toward their mothers in Rafting groups: descriptive statistics

Dependent young activity	$\bar{Y} \pm$ S.E. (g_1)[a]	N
Ride	0.29 ± 0.056 (2.7)	37
Climb	0.18 ± 0.024 (1.6)	42
Contact	0.27 ± 0.053 (3.0)	34
Greet	0.11 ± 0.012 (0.8)	25
Nuzzle[b]	0.12 ± 0.024 (1.2)	24
Nurse	1.94 ± 0.109 (0.8)	146

[a] $\bar{Y}$ = mean, S.E. = standard error (both in min), and g_1 = coefficient of skewness. All estimates of skewness deviate significantly from 0 ($p < 0.05$) except Greet. – [b] For dependents nuzzling foreign adults, $\bar{Y}$ = 0.08 (S.E. = 0.014, N = 18).

walruses in Rafting groups (about 20 % of act-type occurrences). It should be emphasized that much of this activity was subtle, and consisted of passive touching, underwater and surface play between dependents, nursing, etc., so the activity level of Rafting herds was deceptively low on casual inspection.

Social activity levels of dependents were higher than for females, which were higher than for males, across major activity classes (Table 4). A factor contributing to the higher level of females than males was the activity levels of dependents. The latter thereby elicited and initiated many interactions with foreign females.

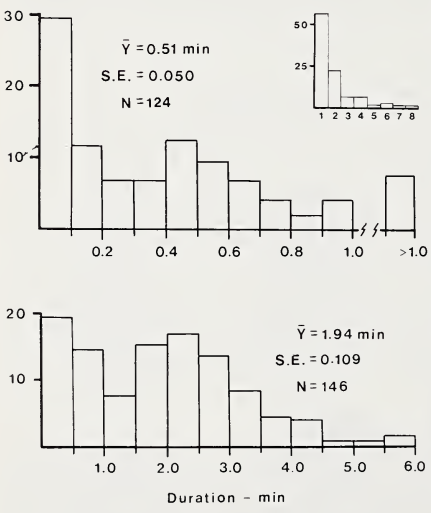

Fig. 5. Frequency histograms of duration of periods between Nursing dives (upper histogram), and durations of Nursing dives (lower histogram). Inset: Frequency histogram of the number of acts between Nursing dives ($\bar{Y}$ = 1.86, N = 124)

Riding behavior of dependent young is pronounced when walruses are moving rapidly away from danger, though we saw none in that context (Burns 1965). Most Riding was casual, and at the offspring's initiative; it often occurred just at the beginning of a female's dive, or during Surface Travelling. In such contexts, it averaged 0.29 min long (Table 5). Females also commonly grasp the calf and dive with it, in the presence of danger, though we did not observe such behavior (Burns 1965; Fay 1982; Mansfield in litt.).

Descriptive statistics for other behavior between females and their offspring are summarized in Table 5. All average about 0.1–0.2 min, with the exception of Nursing, and are strongly right-skewed. No trends suggesting changes with age of offspring are present, though sample sizes are small.

Table 6

Activities of dependents between Nursing dives, compared with activities before and after Nursing bouts

Activity	Frequency (and per cent) of occurrences: Between Nursing dives	Immediately before/after Nursing bouts	Total
Individual restive[a]	134 (59.8)	21 (53.8)	155
Individual active[b]	50 (22.3)	14 (35.9)	64
Social (non-mother)[c]	11 (4.9)	1 (2.6)	12
Social (mother)[d]	29 (12.9)	3 (7.7)	32
Active contact	11	0	11
Nuzzle	11	0	11
Climb	3	1	4
Greeting	2	0	2
Hold	1	0	1
Ride	1	2	3
Totals	224	39	263

[a] Including Bottle, Up, Ventral Float, Back Float, Head Lift. – [b] Including Surface Swim, Shallow Dive, Deep Dive. – [c] Including Threat, Active Contact or Nuzzle foreign walrus, Social Play. – [d] Total occurrences of social behavior directed toward mother (classes as listed).

Nursing

Nursing occurred frequently in Rafting groups, and small groups consisting mainly of Nursing females often formed (Fig. 4). Rarely, females would Nurse while floating horizontally, especially while Back Floating (the latter was the only aquatic posture used by Nursing females in SALTER's [1978] study). Most commonly, females Bottled while their young Nursed vertically upside-down, with only the rear flippers exposed (Fig. 4). Dependents remained submerged for an average of 1.94 min (0.48 min in SALTER's [1978] study), then would return to the surface, Nuzzle or otherwise contact the female, or loll briefly at the surface, before diving to resume Nursing (mean time at the surface between Nursing dives = 0.51 min) (Fig. 5). Dependents commonly interacted with their mothers while at the surface between nursing dives: affiliative and contact behavior occurred in 16.7 % of intervals between Nursing dives, and constituted 12.9 % of acts then. The latter

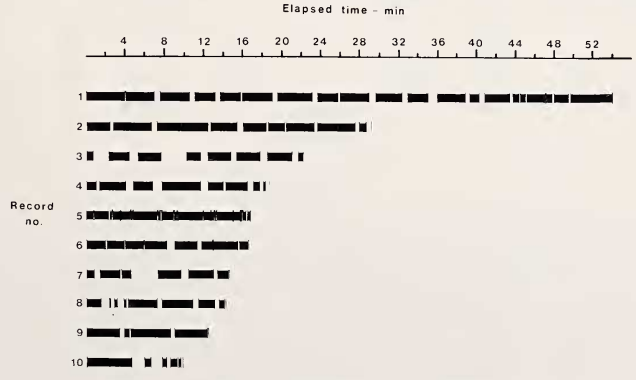

Fig. 6. Summary of the time courses of 10 complete aquatic Nursing bouts. Solid portions of the records represent Nursing dives

figure is about double the overall incidence of social activity by dependents in Rafting groups (6.7 %; Table 4), and the incidence of mother-directed behavior immediately before and after Nursing bouts (7.7 %; Table 6). Despite such complex interactions, most behavioral sequences at the surface between Nursing dives were simple, and more than half consisted of just one act type (inset, Fig. 5).

The time courses of representative Nursing bouts are summarized in Fig. 6. The weighted mean per cent of time below the surface is 81.3 % for the records shown, and is 77.3 % when other data are included (these figures were computed from the initiation of the first complete nursing dive, to the initiation of the last). We obtained estimates for only 25 complete bout lengths. These averaged 11.7 min long (S.E. = 2.16, range = 1.7 – 53.7 min), as compared with 16.0 min for 10 bouts on ice or land noted by SALTER (1978).

Acoustic behavior

In-air sounds of walruses are simple, and most fall into two main structural classes. Bellowing is a loud, repeated tonal cell given by dependent young under numerous circumstances, particularly when troubled (Fig. 7). At high intensity, Bellowing is rapidly and rhythmically repeated (Fig. 7A, B). At lower intensity, Bellows are emitted more slowly and irregularly, are softer, and are often longer. At an extreme, Bellows are emitted singly (Fig. 7C, E). Bellowing occurs in older animals too, primarily during high intensity submission. In comparison with dependent young, their calls are lower in frequency, are

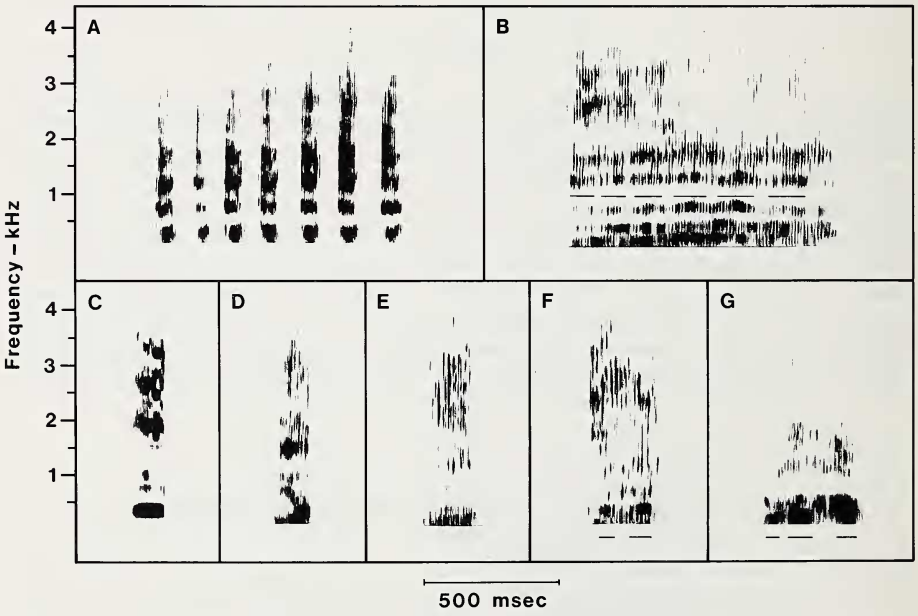

Fig. 7. Sound spectrograms of Bellowing (analyzing filter bandwidth, 300 Hz). A: Part of a loud series by a 3- to 4-year old walrus, being struck by others (high intensity submission); B: Compound series by a juvenile male. Six bellows comprise this series as judged by ear, and as shown by the marks (high intensity submission); C: Monosyllabic Bellow by C2 or C3, while simply walking ahead of its mother (non-submissive context); D: Monosyllabic Bellow by medium-small male, while being threatened (low intensity submission); E: Monosyllabic Bellow by medium male, after being threatened (low intensity submission); F: Bisyllabic Bellow by medium-large male, after being threatened (medium intensity submission); G: Trisyllabic Bellow by small male after being struck (medium-high intensity submission)

more distinctly pulsed, are longer, are generally given more slowly and in briefer series, and often merge (Fig. 7). Otherwise, grading in Bellows of adults parallels that for young. For further discussion of contexts in which Bellowing occurs, see Miller (1975a, 1975b).

Oral Expirations form the other main class. These range from broad-band snorts and guttural, pulsed coughs to tonal Roars (Fig. 8). Snorts and pulsed expirations are commonest, and are given by threatening walruses before and after striking or feinting, usually while the head is held high in tusk-threat. They are also given by animals when lying down after dominating another, or when simply watching another animal approach or pass by. Multiple expirations are also occasionally given at high intensity (e.g. Fig. 8C, E). Tonal threat calls are associated most often with a dominant's approach toward a recumbent subordinate, and are thus used over longer distances than are snorts and coughs; large males often emit brief tonal Roars after they land, and start moving toward the herd. Nevertheless, they are still short-range signals, rarely being directed over distances of more

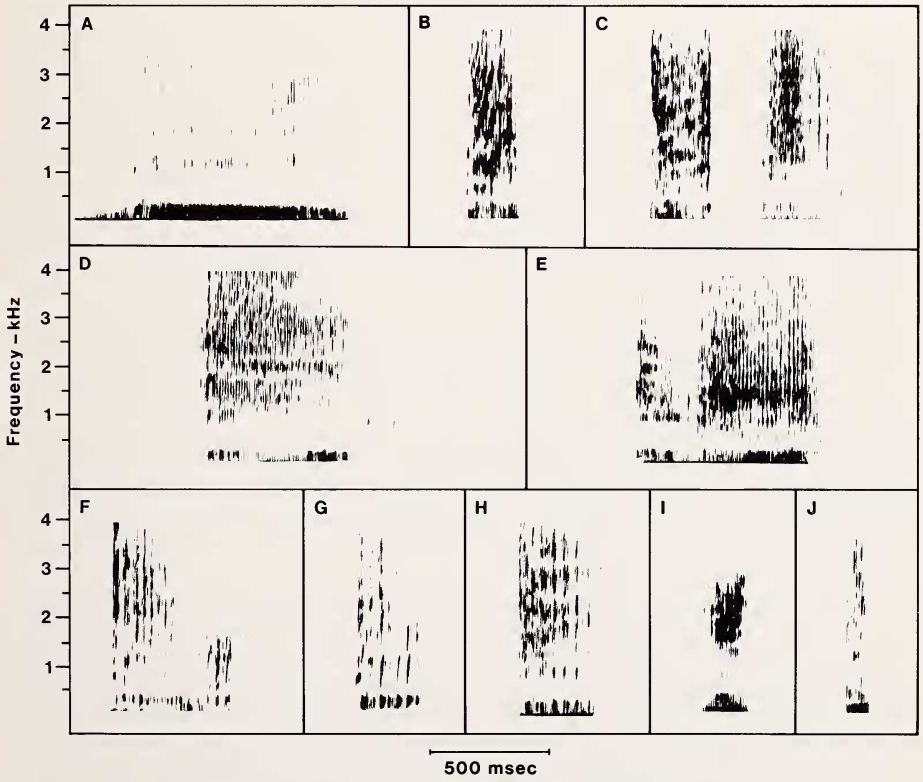

Fig. 8. Sound spectrograms of threatening vocalizations (analyzing filter bandwidth, 300 Hz); A: Long tonal call by medium-large male reared high in tusk treat toward another medium-large male, with smaller tusks; B, C: Single and double broad-band calls by medium-large male toward medium male, while reared high in tusk threat; D: Pulsed broad-band call by large male toward large male, while lying unmoving on side, and in response to latter male's nearby movement; E: Two-part, broad-band call, by large male lying on his side, watching nearby juvenile move; F, G: Guttural call by medium female while reared high in tusk threat, watching small walrus moving near its rump; H: Guttural call by medium male lying on his side, while watching medium-small male move next to him; the call was accompanied by a very weak tusk-threat; I: Grunt by medium male while threateningly standing up in response to the approach of a smaller medium male (unaccompanied by tusk threat); J: Grunt by medium male as adjusting his prone position in response to a small male moving near his rump

than a few meters. Finally, non-submissive walruses often emit single, undirected expirations (usually snorts) when surprised (e.g. when suddenly awakened by being jostled or struck).

Other kinds of sounds are given on and near the hauling ground. These include "whistling", a "rusty door" sound, a "Coke bottle" sound (similar to the sound produced by blowing down the neck of a bottle), knocks, "bongs", prolonged nasal snorts, and a soft tonal call by females toward their offspring (for some discussion of these sounds, see Miller 1975b; Ray and Watkins 1975; Schevill et al. 1966). The calls by females are heard infrequently, perhaps largely because of their softness; the other calls mentioned are associated with aquatic activities, and are mainly given at the water surface.

Discussion

General comments

The number of walruses on or near the hauling grounds during our study was affected proximately by sea ice, polar bears, and man. However, main haulout trends were affected little by these factors, and were likewise influenced immeasurably by the extremes of weather and temperature we observed (the latter two factors certainly affect haulout patterns, however; see Fay and Ray 1968; Mansfield 1958; Miller 1976; Ray and Fay 1968; Salter 1978, 1979). Knowledge of the dynamics and distribution of walruses at all regional hauling grounds is probably necessary to understand trends at a single one. However, it is apparent that continuous access to each hauling ground is not crucial, and that some hauling grounds may remain unused for long periods of time even when walruses are in the vicinity.

Most walruses occurred in groups when in the water. Group size varied according to group activity, and to age and sex of group members. Expectedly, the largest groups were Rafting and the smallest were Travelling. Males tended to occur in small groups, and dependent young (and by extension, females) in larger ones. This trend is only partly explained by the obvious link between females and their offspring, and by the occurrence of Nursing walruses in Rafting groups. Additionally, males tended to be segregated from females with offspring. The means by which segregation is effected are unknown, but its significance probably lies in the different time and energy budgets of the sexes, imposed by the costs of lactation, the need to nurse undisturbed for long periods, differences in food requirements related to body size, etc.

Few data on group size in walruses are available. For Pacific walruses, Fay and Ray (1968) and Fay (1982) summarize published and unpublished data for groups on ice and in the water, and Wartzok and Ray (1980) summarize data on group sizes on ice. These references indicate that walrus groups are largest on land, smaller on ice, and smallest in the water. Of 300 groups noted in the water in March and April, 211 (70 %) contained 1–2 walruses; this compares with 56 % in our study (Fay 1982). Information on size and composition of groups of Atlantic and Pacific walruses feeding and travelling in open water are needed, before the significance of our data, on groups near shore, to walrus social structure can be appraised.

Males were in the minority in both years of study. This too may reflect a sexual difference in schedules, with males spending more time at sea. Estimates of composition of summering herds at other hauling grounds are needed to investigate this. Clearly, to resolve this and other important questions about herd structure and composition (including the relative proportions of dependent young of different ages), simultaneous research at all major regional hauling grounds, and research into feeding ecology near Coats Island, are badly needed.

Social behavior

The high sociality of walruses is expressed in their extreme year-round gregariousness on land and ice, and at sea, and their habit of lying in tightly packed herds when hauled out. Aggressive behavior within herds on land and ice is frequent and time-consuming, especially during early phases of haulout (Miller, 1975b, 1976; Salter 1978, 1979, 1980). The results of such behavior are usually minor, though Salter (1978, 1980) saw one male, bleeding from six tusk wounds, chased out of the water and around a herd on land, then back into the water. We saw nothing comparable. The high levels of agonism within hauled-out herds contrast with the generally amicable behavior in groups at sea. Threats and submission occur there, but are generally brief and mild. This reflects the fact that walruses on land and ice must frequently threaten other animals to gain and defend space, and to prevent themselves from being too crowded; the latter can lead to death, especially of young animals (Fay and Kelly 1980; Fay in litt.). Such considerations do not apply to groups at sea, though extremes of threatening and fighting behavior occur in water during the winter rut, and occasionally among males at other times of year (cf. Salter's observation).

Overt social behavior occupied no more than about 1 % of walruses' time in the water, except for dependent young (and excluding mother-calf behavior), and most occurred in Rafting groups. Dependent young spent about 6 % of their time interacting with walruses other than their mothers, in keeping with dependents' high activity levels and frequent social play. Mother-offspring behavior comprised about a third of females' time, and about half of dependents' time in Rafting groups; comparative figures for walruses on land or ice, and for other pinnipeds, are unfortunately not available. Estimates of terrestrial time budgets of summering Pacific and Atlantic walruses are presented by Miller (1976) and Salter (1978, 1979). It is difficult to make useful quantitative comparisons, because the former study dealt only with males, and the latter recognized very broad behavioral categories for small numbers of animals (maximal herd size of 129).

It has long been recognized that walruses Nurse both in or out of the water, and Loughrey (1959) has mentioned the most commonly used aquatic posture (vertical upright). Our observations indicate that aquatic Nursing is common and significant, and it seems likely that female-offspring pairs are not reliant upon land or ice to Nurse (Fay [1982] reports that even aquatic parturition may occasionally occur). This is also true of the Common Seal, *Phoca vitulina* (Calambokidis et al. 1978; Knudtson 1974), but aquatic nursing is unimportant or undescribed for other phocids. We know of no observations on aquatic Nursing in Otariidae, but it may occur in all sea lion species, and those species of fur seals in which females and their offspring remain together for a year or more and probably feed together at sea (including *Arctocephalus australis*, *A. galapagoensis*, and *A. pusillus*: Bonner 1981; Trillmich 1981; Trillmich and Majluf 1981). However, it seems clear that aquatic Nursing is better developed and commoner in walruses than in any other pinniped species. This development has been promoted by the extreme aquatic specialization of the species and the long female-offspring bond, and has been made necessary by two forces: the absence of attachment to a fixed spatial location for Nursing, in contrast to Otariidae; and the unpredictability of available substrate and suitable weather for haulout. Finally, it must be mentioned that adoptive behavior may be widespread and highly important to Pacific walruses (Eley 1980; Fay 1982). Our observations shed no light on this phenomenon for Atlantic walruses, but the possibility should be considered in future studies.

Acknowledgements

Particular thanks are due to Dr. A. W. Mansfield, for encouraging and making the 1978 study possible, and for providing further support in 1980. Many other people aided this work, from preliminary organization through data analysis, and we thank them all: K. Kovacs, A. Hussey, B.

MacCullogh, J. Nakoolak, P. and K. Rawlings, and G. Watt. Financial support was generously given by the National Geographic Society and the World Wildlife Fund (Canada); other support was from the Natural Sciences and Engineering Research Council of Canada (individual operating grant to E. H. Miller, York University) and the Smithsonian Institution Fluid Research Fund. We thank Drs. F. H. Fay, A. W. Mansfield, and D. G. Wartzok for their detailed and constructive comments on drafts of this paper.

Zusammenfassung

Verhalten vom Atlantischen Walroß, Odobenus rosmarus rosmarus (L.) auf Coats Island, N. W. T. (Kanada) im Sommer

Walrosse nutzen verschiedene Rastplätze auf und in der Umgebung von Coats Island im nördlichen Teil der Hudson Bay. Von bestimmten Rastplätzen können sie aus unbekannten Gründen längere Zeit abwesend sein, und häufig verbleiben sie sogar dann im Wasser, wenn sie an Land gehen könnten. Eine große Gefahr stellen wahrscheinlich Eisbären für junge Walrosse in diesem Gebiet dar. Viele Beweise von Eisbärüberfällen wurden gefunden.

Weibliche Walroßherden waren auf dem Festland und in der Nähe der Küste vorherrschend. Weibchen mit Kälbern neigten dazu, in der Nähe der Küste an Land zu bleiben, solche mit Jungtieren anderer Altersklassen gingen weiter landeinwärts. Das könnte mit Überfällen durch Eisbären zusammenhängen.

Im Wasser nahe der Küste waren die Gruppen durchschnittlich 3,6 Walrosse stark. Die Gruppengröße nahm zu, wenn die Tiere wenig aktiv waren, umherziehende Gruppen waren am kleinsten. Weibchen mit Nachwuchs neigten dazu, sich von den Männchen abzusondern. Sie formierten wenig aktive Gruppen, in denen aquatisches Säugen stattfand. Einzelaktivitäten und soziale Aktivitäten innerhalb der Gruppen werden beschrieben und gemessen. Ältere, noch vom Muttertier abhängige Jungtiere werden gewöhnlich im Wasser gesäugt. Dabei zeigt ihre Bauchseite nach oben. Die Säugeperioden betragen durchschnittlich 12 Minuten.

In die Luft abgegebene Laute werden beschrieben. Die meisten zeigen ein ausgedehntes Frequenzspektrum. Unterschiedliche Lautäußerungen werden als Drohung eingesetzt. Große Bedeutung hat das Brüllen. Es wird bei vielen Gelegenheiten von subadulten Individuen eingesetzt, von adulten Tieren nur dann, wenn sie Unterwerfung zum Ausdruck bringen.

Literature

Bonner, N. (1981): Southern fur seals *Arctocephalus* (Geoffroy Saint-Hilaire and Cuvier, 1826). In: Handbook of Marine Mammals, vol. 1. The Walrus, Sea Lions, Fur Seals and Sea Otter. Ed. by Ridgway, S. H.; Harrison, R. J. 161–208. New York: Academic Press.

Burns, J. J. (1965): The walrus in Alaska. Juneau, Alaska: Alaska Dept. Fish and Game.

— (1970): Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. J. Mammalogy **51**, 445–454.

Calambokidis, J. et al. (1978): Chlorinated Hydrocarbon Concentrations and the Ecology and Behavior of Harbor Seals in Washington State Waters. Olympia, Washington, USA: Evergreen State College.

Davis, R. A.; Finley, K. J.; Richardson, W. J. (1980): The Present Status and Future Management of Arctic Marine Mammals in Canada. Yellowknife, N. W. T., Canada: Science Advisory Board of the Northwest Territories.

Eley, T. J., Jr. (1978): A possible case of adoption in the Pacific walrus. Murrelet **59**, 77–78.

Fay, F. H. (1981): Walrus *Odobenus rosmarus* (Linnaeus, 1758). In: Handbook of Marine Mammals, vol. 1. The Walrus, Sea Lions, Fur Seals and Sea Otter. Ed. by Ridgway, S. H.; Harrison, R. J. 1–23. Academic Press: New York.

— (1982): Ecology and Biology of the Pacific Walrus *Odobenus rosmarus divergens* Illiger. U. S. Dept. of the Interior, Fish and Wildlife Service, North American Fauna Series 74.

Fay, F. H.; Kelly, B. P. (1980): Mass natural mortality of walruses *(Odobenus rosmarus)* at St. Lawrence Island, Bering Sea, autumn 1978. Arctic **33**, 226–245.

Fay, F. H.; Ray, C. (1968): Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). I. Evidence from thermoregulatory behavior. Zoologica **53**, 1–18.

Kiliaan, H. P. L.; Stirling, I. (1978): Observations on overwintering walruses in the eastern Canadian high arctic. J. Mammalogy **59**, 197–200.

Knudtson, P. M. (1974): Mother-pup behavior within a pupping colony of harbor seals *(Phoca vitulina richardi)* in Humboldt Bay, California. M. A. thesis. Humboldt, Calif., USA: Calif. State Univ.

Loughrey, A. G. (1959): Preliminary Investigation of the Atlantic Walrus *Odobenus rosmarus rosmarus* (Linnaeus). Can. Wildl. Serv. Manage. Bull. Ser. **1**, No. 14, 1–23.

Mansfield, A. W. (1958): The Biology of the Atlantic Walrus *Odobenus rosmarus rosmarus*

(Linnaeus) in the eastern Canadian arctic. Ph. D. thesis. Montreal, P. Q., Canada: McGill University.

Miller, E. H. (1975a): A comparative study of facial expressions of two species of pinnipeds. Behaviour **53**, 268–284.

— (1975b): Walrus ethology. I. The social role of tusks and applications of multidimensional scaling. Can. J. Zool. **53**, 590–613.

— (1976): Walrus ethology. II. Herd structure and activity budgets of summering males. Can. J. Zool. **54**, 704–715.

— (1982): Herd organisation and female threat behaviour in Atlantic walruses *Odobenus rosmarus rosmarus* (L.). Mammalia **46**, 29–34.

Ray, C.; Fay, F. H. (1968): Influence of climate on the distribution of walruses, *Odobenus rosmarus* (Linnaeus). II. Evidence from physiological characteristics. Zoologica **53**, 19–32.

Ray, C.; Watkins, W. A. (1975): Social function of underwater sounds in the walrus *Odobenus rosmarus*. Rapp. P.-v. Reun. Cons. int. Explor. Mer **169**, 524–526.

Reeves, R. R. (1978): Atlantic Walrus *(Odobenus rosmarus rosmarus)*: a Literature Survey and Status Report. U. S. Dept. of the Interior, Fish and Wildlife Service, Res. Report 10.

Salter, R. (1978): Normal Behaviour and Disturbance Responses of Walruses (*Odobenus rosmarus* L.) during Terrestrial Haul-out, Eastern Bathurst Island, N. W. T., July–August 1977. Toronto, Ontario, Canada: Report to Polar Gas Env. Program by LGL Ltd., Env. Res. Assoc.

Salter, R. E. (1979): Site utilization, activity budgets, and disturbance responses of Atlantic walruses during terrestrial haul-out. Can. J. Zool. **57**, 1169–1180.

— (1980): Observations on social behaviour of Atlantic walruses (*Odobenus rosmarus* L.) during terrestrial haul-out. Can. J. Zool. **58**, 461–463.

Schevill, W. E.; Watkins, W. A.; Ray, G. C. (1966): Analysis of underwater *Odobenus* calls with remarks on the development and function of the pharyngeal pouches. Zoologica **51**, 103–106.

Smith, T. G. (1980): Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Can. J. Zool. **58**, 2201–2209.

Stirling, I. (1983): The evolution of mating systems in pinnipeds. Spec. Publ. Amer. Soc. Mamm. 7, 489–527.

Trillmich, F. (1981): Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. Behaviour **78**, 21–42.

Trillmich, F.; Majluf, P. (1981): First observations on colony structure, behavior, and vocal repertoire of the South American fur seal (*Arctocephalus australis* Zimmermann, 1783) in Peru. Z. Säugetierkunde **46**, 310–322.

Wartzok, D.; Ray, G. C. (1980): The Hauling-out Behavior of the Pacific Walrus. U. S. Marine Mammal Commission, Rep. MMC-75/15, 46 pp.

Authors' addresses: Dr. E. H. Miller, Vertebrate Zoology Division, British Columbia Provincial Museum, Victoria, British Columbia, Canada, V8V 1X4, and Biology Department, University of Victoria, Victoria, British Columbia, Canada, V8W 2Y2, and Dr. D. J. Boness, National Zoological Park, Smithsonian Institution, Washington, D. C. 20008 USA